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The effects of spatial habitat configuration on recruitment, growth and population structure in arctic Collembola

Abstract The population density and demography of five species of arctic Collembola were studied in a naturally patchy habitat, consisting of *Carex ursinae* tussocks with varying degrees of isolation. Focal predictor variables were those describing the spatial configuration of tussocks, including tussock size and isolation and the amount of habitat (cover) at a 1-m^2 scale surrounding each tussock population. The Collembola populations were heavily influenced by environmental stochasticity in the form of winter mortality and summer drought, and the influence of patchiness on population characteristics was evaluated in this context. The five species showed very different responses to the structuring effect of the habitat, depending on life history characteristics, mobility and habitat requirements. Population density was highly variable in both time and space. Spring densities indicated larger winter mortality compared to observations from a previous study, and the snow- and ice-free season from June to August only resulted in population growth for *Folsomia sexoculata*. In the other species, adult mortality must have been high as there was no net population growth despite observed reproduction. The exception was *Hypogastrura viatica*, whose population decline was more likely to have been the result of migration out of the study area. Cover was the most important variable explaining density. No pure area or isolation effects at the tussock level were detected, even in areas with very low habitat cover. Drought was probably an important mortality factor, as July was particularly warm and dry. Due to qualitative differences in the tussocks and the matrix substrate, desiccation risk would be higher during dispersal between tussocks. We suggest that increased dispersal mortality gave the observed pattern of increased density in relation to cover, both in general and in *F. quadrioculata*, an opportunistic species otherwise known for rapid population growth. *Onychiurus groenlandicus*, which had a similar density response to cover, may also be influenced by a rescue effect sustaining densities in areas with high cover. The cover effect can be viewed as a large-scale factor which encompasses the general spatial neighbourhood of each tussock, where inter-population processes are important, as opposed to internal patch dynamics.

Introduction

The effects of habitat patchiness or fragmentation can be analysed at different scales: oriented towards distribution patterns in larger systems of habitat patches, or towards population processes within a single patch or a few patches. At the patch system level, much effort has gone into studying extinction-colonization dynamics, based on the theory of island biogeography (MacArthur and Wilson 1967) or metapopulation dynamics (Levins 1969, 1970). In this context, habitat fragmentation has been viewed as a threat to natural populations or species diversity in general as increasingly small fragments create smaller populations, each with an elevated risk of extinction (Wilcox and Murphy 1985; Quinn and Hastings 1987; Rolstad and Wegge 1987; Burkey 1989; Ims and Stenseth 1989). The metapopulation theory is a powerful analytical framework for extinction-colonization dynamics and patch system scales (see e.g. Levins 1969, 1970; Hanski and Gilpin 1991; Nee and May 1992; Hanski and Simberloff 1997). However, the assumptions behind the metapopulation approach limit its application, especially

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concerning the scale of fragmentation (Hanski and Simberloff 1997). In systems where extinction-colonization dynamics are less important, or where the dynamics of individual patches are coupled, metapopulation theory is not appropriate unless modified to accommodate these processes. To develop a mechanistic understanding of the underlying biological processes, the metapopulation approach alone is not sufficient. Studies at the patch level focusing on demographic processes will in many cases be needed, combined with a system-level approach uncovering properties not directly apparent from metapopulation theory (Ims and Yoccoz 1997).

Patchiness occurs naturally in most habitats and at several scales (Kotliar and Wiens 1990), and many natural populations are obviously able to exploit and survive in fragmented habitat systems over time. In arthropods, ephemeral habitats and their rather specialist species have been studied, e.g. invertebrate communities in temporary pools (Kitching and Beaver 1990), dung and carrion insects (Hanski and Kuusela 1977; Hanski 1990), fruit flies (Rosewell 1990; Shorrocks 1990) and species of *Daphnia* inhabiting temporary rock pools (Hanski and Ranta 1983). Ephemeral habitats and the species exploiting them constitute a special case, as the habitat itself appears and disappears at quite fast rates (often within one generation). Studies of natural populations in more permanently fragmented habitats (or on a time scale relevant to a larger group of species) can give a better basis for understanding variability in population structure and life history strategies. The interaction between species and habitat will have two aspects: on one hand, species characteristics related to, for instance, mobility or life history strategies, will determine the ability to utilize patchy habitat, and on the other hand, the habitat itself may shape the species' development in evolutionary time (e.g. Southwood 1977; Leinaas and Fjellberg 1985; Goodman 1987; Simberloff 1988; Wiens 1989; Ims 1990; Caughley 1994; Hanski and Simberloff 1997; Andreassen et al. 1998). Obviously there will often be a sharp difference between species adapted to naturally occurring patchiness, and those faced with habitat fragmentation enforced on them by human exploitation. At least in vertebrates, behavioural flexibility may counteract the effects of fragmentation (Lott 1984; Wolff et al. 1997).

Here we present a study of a species assemblage of arctic Collembola in a naturally patchy habitat. The aim is to explore how different species exploit and are affected by the same spatial habitat structure, by a thorough analysis of population density and demography. We focus on the following questions. Which spatial aspects of patchiness are influential? How do the effects of patchiness relate to other influences on population dynamics, e.g. environmental stochasticity? For instance, the relative effects of habitat loss, reduced patch size and increased isolation in relation to density and occurrence of organisms have been analysed in a number of bird and mammal species (Andrén 1994). The majority of studies showed that the absolute cover of habitat was very influential, and that effects of spatial configuration, measured as patch size and isolation, only appeared below a threshold of habitat cover. Whether habitat cover is the best predictor for other species and spatial scales needs further study.

In a previous study, we documented widely differing, species-specific patterns in the demography and density of Collembola inhabiting the same patchy habitat (Hertzberg et al. 1994). The study was based on an initial classification of the habitat into low, medium or high levels of patch isolation, without patch-specific data. Methodologically, this approach could only give an overall description of species distributions and density in relation to a roughly defined isolation gradient, and left many questions unanswered. In this study, we have randomly selected local populations in single patches as our study unit, and patch-specific spatial characteristics, cover and to some extent quality have been quantified. We present analyses on how demography and density are related to a range of habitat parameters in the five dominant species (*Folsomia sexoculata, F. quadrioculata, Hypogastrura longispina, H. viatica* and *Onychiurus groenlandicus*).

Materials and methods

Study area

The study area is situated near Ny-Ålesund on Spitsbergen, Svalbard (78°55′N, 11°59′E), and consists of a field of *Carex ursinae* tussocks, situated near a freshwater lagoon with occasional sea water influx. The tussocks are embedded in a matrix of bare mineral soil covered with a layer of cyanobacteria. The tussocks are the preferred habitat for Collembola (Hertzberg et al. 1994). The *Carex* vegetation begins 2–3 m from the shore and stretches about 15 m inwards along a gentle slope with about 20 cm elevation from the lowest to the highest point. Some saltmarsh grass *Puccinellia phryganodes* is found below the tussock belt and scattered between the tussocks. Tussock (patch) sizes range between 35 and 70 cm^2, with a height of 1–2 cm and an organic layer 1 cm deep. They form a spatial gradient of patch isolation with decreasing distance (from 40–60 cm to <5 cm) between them from the shore and upwards. The soil in the area is salt influenced with high sodium concentrations ranging from 28–40 mg per 100 g dry soil near the lagoon shore, to 2–7 mg per 100 g dry soil above the study area (Liengen and Olsen 1997).

Sampling procedure

The study area was divided into squares of 1 m^2 area, measuring 8×15 m in total. Within each square, the number of tussocks was counted and the square classified according to three groups of tussock density: 1–15 tussocks, 20–35 tussocks, >50 tussocks. Within each group, ten squares were drawn randomly for sampling, hereafter named the study squares. A corer with a 10-cm^2 sampling area was used to collect one soil sample from a tussock and one sample from the cyanobacteria cover in each study square.

Timing of sampling was planned to cover the entire growing season. The first sampling was done on 21 June, immediately after snowmelt. This ensured that no reproduction and hardly any growth had occurred prior to sampling. The size distribution in our June samples represents the overwintering animals. The second collection on 19 August was done after recruitment (egg hatch) had ceased. Changes in density and size distribution would then reflect recruitment, mortality and individual growth over the summer. The samples were stored in a cool room (2°C) until extraction.

After sampling, each square was photographed from directly above. The photos were enlarged and a digitalised map was made of each square (MapGrafix), showing the outline of all tussocks. Based on the maps, data on size and circumference of all tussocks, distances between tussocks and percentage cover of tussock vegetation were obtained. A thermologger measuring the soil temperature at hourly intervals was installed in the study area, with two thermocouplers in tussocks and two in the cyanobacteria layer between tussocks. Climatic data for Ny Ålesund were provided by the Norwegian Meteorological Institute.

Sample treatment

All soil samples were taken to the laboratory at the University of Oslo for immediate dry extraction of collembolans, in a slightly modified high-gradient extractor (Leinaas 1978; Macfadyen 1961). Extraction was initiated within a week, to prevent population growth in the samples. Samples were preserved in benzoic acid. In each sample, all individuals were identified to species, counted and body length measured at 25× magnification under a stereomicroscope. Length was determined at size class intervals of 0.08 mm. The smallest size class used was 0.39 mm and the largest individual measured 2.08 mm. To obtain sufficient sample for the analyses of recent recruitment, the two smallest size classes (0.39–0.55 mm) were lumped and defined as recruits, i.e. newly hatched individuals.

The June soil samples were used for measuring soil conductivity as well. After extraction of collembolans, the samples from the cyanobacteria cover near each sampled tussock were prepared for measurements of conductivity. Conductivity was chosen as a measure of total salt content in the soil. After drying the samples, 4 g of soil were taken from each and dissolved in 40 ml distilled water. The samples were left overnight at 25°C and the solution was filtered. Conductivity was measured in the filtrate using a CMD80 conductivity meter.

Statistical analysis

Two sets of analyses were done of each species: (1) analysis of density, and (2) analysis of demographic patterns, including recruitment and cohort structure. For both sets of analyses concerning the effects of habitat variables, we first considered which model fitted best the data, using Akaike's selection criterion (AIC; Akaike 1981). However, this made the comparison between species and periods difficult, as different sets of variables were selected. We chose therefore to consider the same model, always including the most essential predictor variables Month, Cover, Distance and Area and then comparing the coefficients. Having unnecessary variables (i.e., those that would not have been included according to the AIC) in the model should not bias the estimates for the other variables, but only reduce the precision of the estimates (Burnham and Anderson 1992). On the other hand, models that were too simple would have provided biased estimates of the regression coefficients.

Analysis of density

These analyses, which applied Poisson regression models to total sample counts, served to describe the patterns of tussock-specific density in relation to habitat variables. Inspection of the residuals and the value of the residual variance indicated that the residual variation was larger than expected under a Poisson model. A constant overdispersion factor (i.e., using quasilikelihood estimation; McCullagh and Nelder 1989) provided a satisfactory fit to the data. In some cases, a few individual observations had very large residuals, and we fitted the same models with and without these observations to check the robustness of the analysis.

Analyses of demography

Analyses of demography included two aspects of size distributions. Firstly, there was a fairly sophisticated analysis of the cohort structure. This reflects the results of demographic processes in the populations during a period similar to the life span of the species, and would be the ultimate goal of demographic analyses. However, different cohorts are not always possible to identify, and comparisons at the tussock level require high densities of animals. Due to these limitations, we also made a simpler analysis of recent reproduction, defined as the fraction of newly hatched animals in each sample. This could be done on all samples and therefore was a useful parameter to detect habitat variables that might affect the demography of a population. However, this analysis does not take the reproduction over the whole season into account, only the most recent recruitment. Thus, the significance of such relationships may be less evident than a comprehensive cohort analysis.

Cohort structure The size (length) distributions were analysed assuming they derived from a k-components normal mixture, each component representing a cohort. In all samples, assuming one or two components was satisfactory. Arctic Collembola become reproductively mature at a certain size, and most arctic species reproduce within a restricted period in the summer (Addison 1981; Birkemoe and Sømme 1998; Birkemoe and Leinaas 1999; K. Hertzberg, R.A. Ims and H.P. Leinaas, personal observations). This reproduction pattern will be reflected in rather distinct cohorts (generations), evident as peaks in the size distribution. In contrast, continuous reproduction in the ice-free season will result in a more unimodal or even size distribution. The analysis of cohort structure should therefore give a more biologically realistic description of demography than the initial arbitrary definition of size classes.

The following statistical model for the probability density function of size, x, was used:

$$f(x) = \sum p_i f_i(x;(\mu_i,\sigma_i)) \quad i = 1,2$$

where f_i is the probability density function of a normal distribution with mean μ_i and standard deviation σ_i, and the p_is are the proportions of the two cohorts ($p_1+p_2=1$). We used statistical methods for the analysis of mixture distributions to estimate the proportions p_i belonging to each cohort as well as the mean and variance of each distribution (see Titterington et al. 1985 for a review). We used Bayesian methods, as more classical approaches based on likelihood theory do not work well (Robert 1996). Bayesian methods assume prior distributions for the different parameters (p_i, μ_i, σ_i), but the influence of this choice is reduced by assuming vague (uninformative) prior distributions. The statistical model assumed a flat prior distribution for the proportions (Dirichlet distribution), as well as uninformative normal priors (prior means equal to 0.5 and 1, and variances at least 2) for the means and uninformative prior distribution based on the Gamma distribution for the variances. For large samples (for example, pooled samples from one period), this proved adequate. For smaller samples (i.e., for less than *c.* 30 individuals), we assumed equal variance for the two cohorts, and if necessary we used more precise priors for the means with variances as small as 0.5. Given that the average sizes were always between 0.5 and 1 mm for the first cohort, and between 0.8 and 1.5 mm for the second, this did not affect the estimates much (see Results). Calculations were done in BUGS (Gilks et al. 1996), using the parameterization of Mengersen and Robert (1996). The output of BUGS calculations was analysed in CODA (Best and Vines 1995), in order to calculate the standard deviations of estimated parameters, as well as for checking the convergence of the numerical algorithm. We assessed the adequacy of the fitted distribution by comparing it graphically to an empirical distribution smoothed using a non-parametric kernel. The latter was implemented in S-Plus, and the kernel window width was chosen by cross-validation (Venables and Ripley 1994). There was no simple way of testing for the number of components in the mixture (Mengersen and Robert 1996), as the likelihood-ratio test does not behave even approximately well in this case (Thode et al. 1988). We used instead a graphical comparison, mainly based on the existence of bimodality in the smoothed empirical distribution.

Distinct cohorts could not always be identified. Where confidence intervals of the estimates of body size of the two cohorts overlap, the two cohorts could be regarded as one. When the confidence intervals of estimates of dominance (proportion of population) are wide this describes an unclear population structure and should be interpreted with care. Overlapping size estimates may indicate a continuous structure or unimodal distribution where distinct generations cannot be identified. This happens either when reproduction is continuous throughout the summer, or when the population consists of one generation only. Interpretation of the estimates was further aided by visual inspection of the empirical size distribution.

Many of the tussock samples contained too few individuals (fewer than 15) to allow cohort estimation at the tussock level. For all species we therefore present the cohort estimates based on pooled tussock samples for each time period. Where sample sizes at the tussock level allowed it the effects of the variables Distance, Area, Cover and Month on the cohort proportions and cohort mean sizes were estimated by fitting a linear model by weighted least squares (Rao and Toutenburg 1995). The weights were the inverse of the estimated variances provided by the Bayesian analysis. Samples allowing for this analysis were available only for *H. viatica* and *F. quadrioculata*.

Where two distinct cohorts could be identified, the dominance relationship between cohorts was analysed in relation to habitat variables and time (Month) in a logistic regression following the methods described for the recruitment analysis. The logistic regression analysis on cohort structure could only be done in *H. viatica* and *O. groenlandicus*. In the other species, further analysis on cohort ratios was precluded by large overlap between cohorts, which makes any separation based on a single cutpoint highly unreliable: a small change in the average value of one cohort may have an overly large influence on the proportions estimated from the single cutpoint.

Recruitment In this analysis we applied logistic regression models (Agresti 1990) to the proportion of recruits in the samples (recruits/total). For all species except *F. sexoculata*, the residual deviance was significantly larger than expected under the hypothesis of a binomial distribution. The large differences in sample size precluded the simple use of an overdispersion (scale) factor (Cox and Snell 1989), and we have therefore implemented the quasi-likelihood estimation approach corresponding to model II of Williams (1982). Model II assumed that var(R_i) was equal to $v_i w_i^{-1}$, where v_i is the binomial variance (i.e. $m_i\theta_i(1-\theta_i)$), and where w_i^{-1} is $1+\phi(m_i+1)$. ϕ was estimated iteratively using the method of moments, based on the expected χ^2 being equal to its number of degrees of freedom. Some analyses showed one or two observations to be very poorly fitted by the model, and therefore the model was also fitted without these observations to check the robustness of the conclusions.

Results

System characteristics

Climatic factors

The summer of 1993 was warmer than usual. The mean temperatures of July and August in 1993 were 5.8°C and
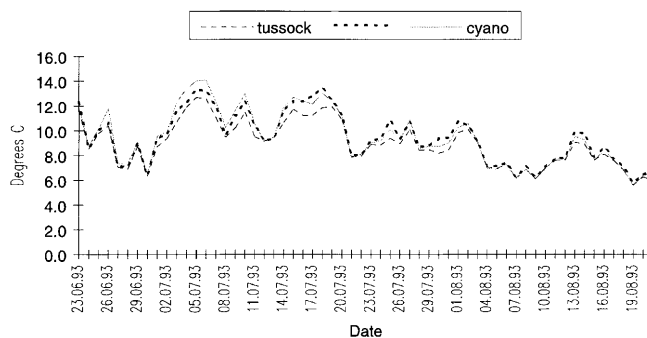

Fig. 1 Mean daily temperatures 23 June–21 August 1993 in two tussocks and one site in the cyanobacteria cover

5°C respectively, whereas the norm is 4.7°C and 3.9°C. July, which covers the main period of population growth, was also very dry, with a precipitation in July of only 8 mm, against a norm of 29 mm. In August the precipitation was 64 mm, against a norm of 40 mm. The log of the temperature at ground level showed generally higher values than the air temperature with two particularly warm spells at the beginning and end of July (Fig. 1). There were no consistent temperature differences between the tussocks and the cyanobacteria cover, although this result hinges on few measurement points.

Habitat variables

There was a gradient upwards in the study area in reduced soil conductivity and increased vegetation cover (conductivity/cover vs. position in gradient; Fig. 2). Tussock area and circumference also increased in an upward trend in the study area: tussocks not only increased in numbers, but were also of a larger size. The distribution of nearest neighbour distances and mean inter-tussock distances showed that tussock isolation had a wider range at the lower end of the gradient, and did not follow a linear increase. Isolation was more weakly related to cover and conductivity.

Analyses of density

Sample counts obtained from the tussocks were much higher than those taken from the cyanobacteria matrix between the tussocks (Table 1). *O. groenlandicus* was most rare, while *H. viatica* was most common in the matrix. Below we analyse the sample counts from the tussocks.

Table 1 Total number of five species of Collembola (*Folsomia sexoculata, F. quadrioculata, Hypogastrura longispina, H. viatica* and *Onychiurus groenlandicus*) caught in all samples in tussocks and on the cyanobacteria surface in June and August

Species	Tussocks, June (n=30 samples)	Tussocks, August (n=26 samples)	Cyanobacteria, June (n=30 samples)	Cyanobacteria, August (n=30 samples)
O. groenlandicus	404	606	2	4
F. sexoculata	310	490	11	7
F. quadrioculata	913	1012	15	38
H. longispina	206	298	45	21
H. viatica	1211	791	356	223

Fig. 2 Scatterplots of habitat variables in all study squares: conductivity, %cover, sample tussock area (cm²) and circumference, nearest-neighbour distance (cm), mean tussock area (cm²) and mean inter-tussock distance (cm). *Position in gradient* describes distance (m) from the lower edge of the study area (3 m from the shore of the lagoon) to each study square, where the first square (i.e. with highest degree of isolation) is set to 1 m
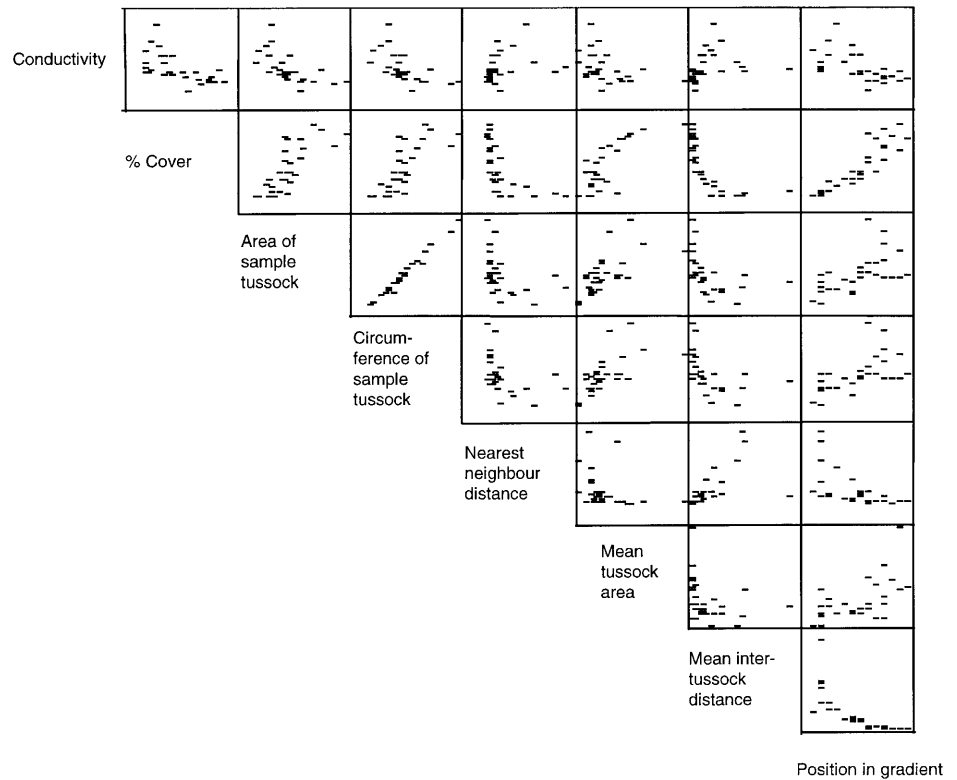

Table 2 The effect of habitat variables and time in season on total density and density of recruits and recruitment (ratio of newly hatched vs. large individuals) in *O. groenlandicus, F. sexoculata, F. quadrioculata* and *H. longispina*. For *O. groenlandicus,* analysis on cohort ratio (ratio of the estimated smallest cohort versus the larger) is also presented. For the *Folsomia* species and *H. longispina*, separate cohorts could not be estimated. The estimates are regression coefficients±SEs (taking into account overdispersion). Significant (*P*<0.05) coefficients in *bold*. The residual deviance (before correcting for overdispersion) is given for the model with all four variables included

| Species	Population parameter	Variable				
		Distance	Area	Cover	Month	Residual deviance
O. groenlandicus	Total density	–0.067±0.052	0.004±0.004	**0.045±0.016**	–0.11±0.31	610.5, *df*=51
	Recruitment	0.042±0.048	–0.004±0.004	**0.036±0.018**	**0.72±0.35**	59.8, *df*=35
	Cohort ratio	**–0.069±0.034**	0.007±0.005	**0.034±0.016**	**0.73±0.32**	69.9, *df*=51
F. sexoculata	Total density	–0.011±0.007	–0.000±0.005	**–0.128±0.023**	**0.65±0.25**	469.6, *df*=51
	Recruitment	0.009±0.006	0.006±0.005	0.013±0.024	**1.09±0.43**	37.1, *df*=39
F. quadrioculata	Total density	–0.029±0.026	0.001±0.003	**0.048±0.011**	0.31±0.23	1324.7, *df*=51
	Recruitment	**0.044±0.021**	–0.006±0.005	–0.016±0.016	**1.29±0.32**	286.6, *df*=48
<u>*H. longispina*</u>	Total density	0.003±0.008	0.005±0.004	–0.008±0.014	0.44±0.28	351.8, *df*=51
	Recruitment	0.011±0.010	0.004±0.005	0.012±0.019	0.13±0.39	87.6, *df*=49

In *O. groenlandicus* the densities were generally low, with two-thirds of the samples with ≤10 animals (and none individual in one-third) (Fig. 3). The density did not change significantly over the summer, but was positively related to the extent of *Carex* cover (Table 2). However, between-sample heterogeneity that could not be explained by the regression models was large (residual deviance in Table 2).

The density of *F. sexoculata* was similarly low (Table 1, Fig. 3). However, it increased over summer and was negatively related to *Carex* cover (Table 2). Also for this species the model fit was only mediocre.

F. quadrioculata had generally a high level of occurrence (Fig. 3), but did not increase significantly over the summer. As for *O. groenlandicus*, the density increased as cover increased (Table 2). But the model fit was poor, indicating a large, unexplained between-tussock heterogeneity.

H. longispina also had a fairly high level of occurrence, but much lower density than *F. quadrioculata* (Table 1, Fig. 3). There was a tendency for increased density over the summer (Fig. 3), but this was not significant (Table 2). There were no significant variables relat-

Fig. 3 Total density and density of recruits (size class 0.39–0.55 mm) in June and August for 5 species of Collembola (*Folsomia sexoculata, F. quadrioculata, Hypogastrura longispina, H. viatica* and *Onychiurus groenlandicus*). The *abscissa* shows different density classes, *ordinate* shows numbers of sample in different density classes
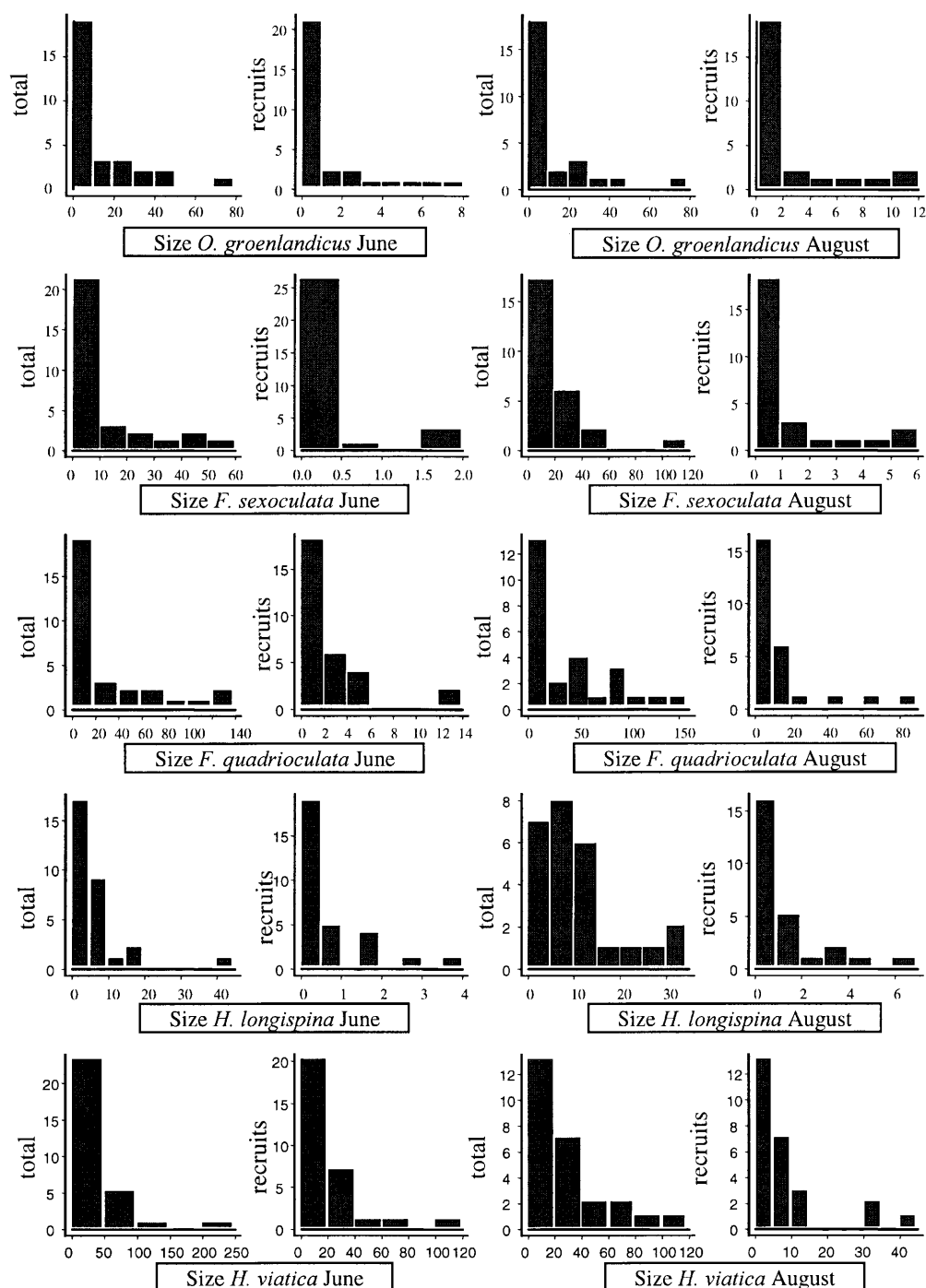
ed to habitat explaining overall density (Table 2). The residual deviances from the regression models were moderate compared to the other species.

H. viatica was most the abundant and widespread species, occurring in all samples (Fig. 3). There was a reduction in density over the summer, but this was also coupled to the habitat variable distance in an interaction term (Table 3). Densities were reduced more in tussocks with short distances between them, i.e. tussocks with low levels of isolation. The large residual error in the Poisson

regression models indicated high unexplained variability between tussocks (Table 3).

Analysis of demography

In *O. groenlandicus* two cohorts could be identified and analysed at tussock level both in June and August (Table 4, Fig. 4). For cohort ratio, both cover and distance were significant (Table 2): dominance of the juvenile cohort in-

Table 3 The effect of habitat variables and time in season on total density, density of recruits, recruitment and cohort ratio in *H. viatica*. The estimates are regression coefficients±SEs (taking into account overdispersion). Significant (*P*<0.05) coefficients in *bold*. The residual deviance (before correcting for overdispersion) is given for the model with all seven variables included except for the recruitment analysis, which had five variables, and the cohort ratio analysis, which had four variables

Variable	Overall density	Recruitment	Cohort ratio
Distance	–0.003±0.013	0.012±0.008	0.011±0.009
Area	0.003±0.004	–0.007±0.005	0.002±0.004
Cover	0.019±0.016	–0.002±0.012	0.017±0.013
Month	–0.040±0.590	0.160±0.270	**–1.290±0.260**
Distance×Month	**–0.051±0.020**		
Area×Month	0.005±0.009	**–0.009±0.004**	
Cover×Month	–0.010±0.025		
Residual deviance	1044.4, *df*=48	97.3, *df*=50	311.8, *df*=51

Table 4 95% confidence intervals for the parameter estimates for the two cohorts; proportion of the population constituted by each cohort and mean body size of cohort. Cohort 1 is the smallest cohort (in size) at any time, cohort 2 the largest

Species	Month	Proportion Cohort 1	Size (mm) Cohort 1	Proportion Cohort 2	Size (mm) Cohort 2
O. groenlandicus	June	0.33–0.53	0.62–0.68	0.47–0.67	1.05–1.17
	August	0.54–0.76	0.65–0.73	0.24–0.46	1.10–1.24
F. sexoculata	June	0.15–0.93	0.82–1.00	0.07–0.85	1.02–1.23
	August	0.35–1.00	0.76–0.89	0.00–0.66	0.88–1.52
F. quadrioculata	June	0.41–0.73	0.69–0.75	0.27–0.59	0.94–1.09
	August	0.17–0.35	0.46–0.51	0.65–0.83	0.70–0.75
H. longispina	June	0.16–0.64	0.61–0.84	0.36–0.84	1.10–1.38
	August	0.74–0.89	0.75–0.81	0.11–0.26	1.19–1.40
H. viatica	June	0.64–0.70	0.55–0.56	0.30–0.36	1.06–1.12
	August	0.27–0.37	0.51–0.54	0.63–0.73	0.92–0.98

creased with decreasing nearest neighbour distance to the sample tussock and with increasing cover. The proportion of the juvenile cohort was highest in August (Table 2). The cohort structure was also qualitatively different in the two months. In June the juvenile cohort comprised overwintering young from 1992. In August a new juvenile cohort had appeared while the juveniles from spring had grown into the adult cohort. Probably few adults from June were still alive. Recruitment increased with cover (Table 2). and it was highest in August. However, the fact that the recruit size class was not included in the size-estimated interval of the juvenile cohort in August implies that hatching had mostly occurred early in the summer and that recruits had grown out of the 0.39–0.55 mm size class.

There was no separation of cohorts in *F. sexoculata* (Fig. 4); estimates of body size overlapped for both June and August (Table 4). The population structure remained constant over the summer, as neither cohort dominance nor size structure changed significantly (Table 4). Recruitment was not influenced by any of the habitat factors, but was significantly highest in August (Table 2). Recruitment was well described by the regression models as there was virtually no overdispersion from a binomial distribution.

In *F. quadrioculata*, estimates of cohort proportions had wide confidence intervals in June, but with some separation of cohort body size (Table 4). In August the two cohorts could be separated more clearly (Table 4). The size distribution still appeared unimodal (Fig. 4), but

had shifted towards smaller mean body size (Table 4). The relative proportion of recruits increased with distance to the nearest patch and from June to August (Table 2). The recruit size class was within the confidence interval for the juvenile cohort both months reflecting continuous reproduction. There were no effects of habitat variables on either proportionate density or size of the two cohorts.

The size distribution of *H. longispina* showed a very flat structure in June (Table 4, Fig. 4). Two cohorts were more clearly separated in August. The population structure of *H. longispina* changed towards increased dominance of juveniles over the summer (Table 4, Fig. 4). There were no significant habitat variables explaining recruitment, and no significant change over time (Table 2). The recruit size class was not included in the confidence interval for the juvenile cohort in August so hatching must have occurred early in the summer.

The development in populations of *H. viatica* followed a distinct pattern of separate cohorts with respect to size and proportions in both June and August (Tables 3, 4, Fig. 4). In June, the population was dominated by a high proportion of overwintered juveniles (Fig. 4). Over the summer, the two cohorts present in June had, respectively, grown in body size (the juveniles from 0.5 mm to 0.9 mm) and disappeared (the adult cohort in August had significantly smaller body size than the one present in June). A new cohort (size 0.5 mm) had appeared in August (Table 4, Fig. 4), representing this year's repro-
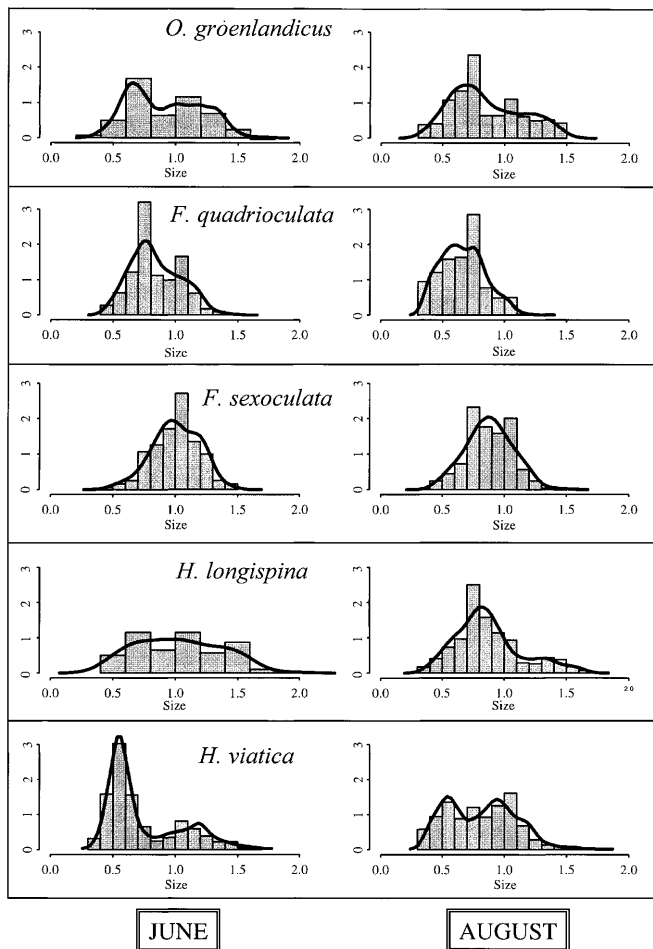
Fig. 4 Kernel estimates (*lines*) and empirical size distribution (mm, *bars*) in June and August. Area under curve=1

duction. There were no effects of habitat variables on either proportionate density or size of the two cohorts. The analysis of recruitment ratio showed an interaction between tussock area and time indicating different effects of the size of habitat patches (sample tussocks) over time. Recruitment was reduced in large tussocks in August compared to June (Table 3). Recruitment was well described by the regression model.

Discussion

The aim of this study was to analyse species-specific patterns of density and demography in a naturally patchy habitat, to consider how spatial heterogeneity may have contributed to different patterns in different species, and to what extent other variables must have been instrumental. The five species showed different responses to temporal and spatial environmental variability, probably dependent on each species' life history characteristics (e.g. overwintering strategies and recruitment patterns) and tolerance to environmental stress. The different species probably also respond differently to the spatial scale of

patchiness in our study system depending on mobility and habitat selection. For example, the two *Hypogastrura* species (especially *H. viatica*) are highly mobile surface-dwelling species, while at the opposite end of a mobility continuum is the sedentary, soil dwelling *O. groenlandicus*. The dichotomy of fine and coarse-grain must in reality represent two ends of a continuum rather than sharp distinctions, as there is a spatial gradient inherent in the study system. The response of a given species may change from fine- to coarse-grained across the gradient. Such changes in habitat exploitation may obscure responses to specific habitat variables.

The species' response to the habitat patch gradient must be seen against the background of two temporal events related to climate. For all species, spring densities (June) showed a marked reduction compared to what we found in August 1992 (Hertzberg et al. 1994), indicating large winter mortality. An important mortality factor in winter is the formation of ice cover (Coulson et al. 2000), which was most extensive in the lower part of the gradient this winter (personal observation). Accordingly, the population reduction was most pronounced in *F. sexoculata*, having its main distribution in this part of the tussock field (Hertzberg et al. 1994). The two *Hypogastrura* species, on the other hand, move higher up on the beach before winter and consequently were least affected by winter mortality. Reproduction during the snow and ice free season from June to August did not result in an expected population growth except in *F. sexoculata*. The most probable cause for this is drought, which has been shown to be a potentially important mortality factor for these species (Hertzberg and Leinaas 1998). The summer of 1993 was very dry, and in our study field this was most pronounced on the upper part, where *Carex* tussocks even started to wilt. The lower part remained more moist, which may explain why *F. sexoculata* appeared most successful in 1993. Moreover, most species displayed considerable heterogeneity in the analyses, indicating very variable population trajectories in the individual tussocks and environmental stochasticity at this level. Theoretical approaches restricted to deterministic equilibrium or expected (average) properties may thus not be applicable.

Cover was the most important variable explaining density. The density of *O. groenlandicus* and *F. quadrioculata* increased with increasing habitat cover, while the density of *F. sexoculata* decreased. This pattern was consistent with the results from the previous summer (1992). In contrast to our initial study (Hertzberg et al. 1994), in the present study we were able to probe the independent effects of spatial variables at the level of individual tussocks. However, no consistent effects of factors such as tussock area or isolation were found. In his review of studies of birds and mammals in fragmented habitats, Andrén (1994) separated effects of habitat loss from effects of the spatial configuration of habitat patches (patch size and isolation). In the majority of studies reviewed, isolation and patch size effects only became significant predictors of species occurrence or density

when the proportion of suitable habitat in a landscape was below around 30% habitat coverage. When habitat coverage was higher, cover was the main predictor and the effects could thus be ascribed to habitat loss. In this study, habitat coverage in the study squares ranged from less than 1% to around 43%. Median cover was 12–14%, and only 23% of the squares had a cover above 30%. We still did not observe clear effects of patch size or isolation on distribution patterns, a pattern not in accordance with the pattern found for birds and mammals. However, Andrén (1994) pointed out that many of the studies he reviewed treated fragmentation at a fine-grained scale, often concerning only a few individuals, and therefore may not be directly applicable to population patterns. This study, on the other hand, undoubtedly treats populations orders of magnitude larger. When effects of patch size and isolation did not appear in our study, at coverage as low as 1–10%, the individual tussocks, and hence tussock population sizes, were probably too large for demographic stochasticity and colonisation-extinction dynamics between different tussocks to become important

The pervasive cover effect can be thus viewed as a relatively large scale factor which encompasses the general spatial neighbourhood of each tussock. The two species *O. groenlandicus* and *F. quadrioculata* have their main distribution in the upper part of the tussock field (Hertzberg et al. 1994). However, the fact that their density and recruitment were positive related to cover may indicate more complex reactions, which also could explain the poor fit of the model for these two species. One such additional factor could be the distance between tussocks. *O. groenlandicus* and *F. quadrioculata* are by far the most drought sensitive of the species studied (Hertzberg and Leinaas 1998; H.P. Leinaas, unpublished work). In this very dry summer, therefore, it seems likely that mortality due to desiccation of dispersing individuals was strongly related to distance between tussocks. Drought stress would be more severe in the cyanobacteria matrix than within the tussocks due to lack of shelter, resulting in an increased mortality of migrating animals. Thus the tussock system may have represented a gradient in mortality corresponding to the amount of inhospitable matrix habitat surrounding the tussocks. However, this interpretation seems most relevant for *F. quadrioculata*, as *O. groenlandicus* to a much smaller extent moves out in the matrix habitat (Table 1; see also Hertzberg 1997).

Even though *F. sexoculata* occupies the part of the *Carex* field with longest distance between tussocks, it is probably little exposed to desiccation during migration. The cyanobacteria matrix in this lowest part of the area is generally quite wet, and in addition it is more drought resistant than its congener *F. quadrioculata* (Hertzberg and Leinaas 1998).

Neither of the two *Hypogastrura* species showed consistent responses in population density to habitat variables. For *H. viatica* this was consistent with the pattern documented in 1992. *H. viatica* is both drought resistant and very mobile so its demography should exhibit low predictability to habitat features at this scale. For *H.*

longispina the change in distribution from a concentration in the more isolated tussocks in 1992 towards more a uniform use of the gradient in the present study is difficult to explain. However, we suggest that it may be the result of migratory activity and/or habitat selection in this mobile (Hertzberg 1997) and moderately drought resistant species (Hertzberg and Leinaas 1998). However, also for this species the details regarding habitat requirements are poorly known.

Densities of all species were generally much lower than previously observed (Hertzberg et al. 1994), so it is not likely that the distribution pattern was a result of competitive interactions between the species either. Other aspects of habitat quality, e.g. changes in substrate or food quality, are probably important, notably for *F. sexoculata* and *H. longispina*. Consequently, more work is needed on the particular habitat requirements of the species and also on their distribution patterns during years with higher population densities.

In conclusion, although the *Carex* tussock system at least superficially represents a stable spatial configuration, temporal external influences interacted with spatial parameters so as to make the ecological effects of such temporal events dependent on space. In particular the effect of drought on Collembola demography seems to have been most severe where the habitat cover was low. Such interactive effects between spatial and temporal environmental variance components are likely to be very condition and species specific as demonstrated in this study. If not explicitly and carefully addressed, for example by experimental designs, the effects of simultaneous spatio-temporal environmental variation will continue to pose problems for establishing general principles of the effects of habitat patchiness on population dynamics.

References

Addison JA (1981) Biology of *Hypogastrura tullbergi* (Collembola) at a high arctic site. Holarct Ecol 4:49–58

Agresti A (1990) Categorical data analysis. Wiley, New York

Akaike H (1981) Likelihood of a model and information criteria. J Econometrics 16:3–14

Andreassen HP, Hertzberg K, Ims RA (1998) Space use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. Ecology 79:1223–1235

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Best NG, Vines SK (1995) CODA Manual, version 0.30. MRC Biostatistics Unit, Cambridge

Birkemoe T, Leinaas HP (1999) Reproductive biology of the Arctic collembolan *Hypogastrura tullbergi*. Ecography 22:31–39

Birkemoe T, Sømme L (1998) Population dynamics of two collembolan species in an arctic tundra. Pedobiologia 42:131–145

Burkey TV (1989) Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserves. Oikos 55:75–81

Burnham KP, Anderson DR (1992) Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullough DR, Barrett RH (eds) Wildlife 2001. Populations. Elsevier, London, pp 16–30

Caughley G (1994) Directions in conservation biology. J Anim Ecol 63:215–244

Coulson SJ, Leinaas HP, Søvik G, Ims RA (2000) Experimental manipulation of the winter surface ice layer: the effects on a high Arctic soil microarthropod community. Ecography 23: 285–300

Cox DR, Snell E (1989) Analysis of binary data. Chapman and Hall, London

Gilks W, Thomas A, Spiegelhalter D (1996) Markov chain Monte Carlo in practice. Chapman and Hall, London

Goodman D (1987) How do any species persist? Lessons for conservation biology. Conserv Biol 1:59–62

Hanski I (1990) Dung and carrion insects. In: Shorrocks B, Swingland IR (eds) Living in a patchy environment. Oxford University Press, New York, pp 127–146

Hanski I, Gilpin ME (1991) Metapopulation dynamics: brief history and conceptual domain. In: Gilpin M, Hanski I (eds) Metapopulation dynamics: empirical and theoretical investigations. Academic Press, San Diego, pp 3–16

Hanski I, Kuusela S (1977) An experiment on competition and diversity in the carrion fly community. Ann Zool Fenn 43:108–115

Hanski I, Ranta E (1983) Coexistence in a patchy environment: three species of *Daphnia* in rock pools. J Anim Ecol 52:263–279

Hanski I, Simberloff D (1997) The metapopulation approach, its history, conceptual domain and application to conservation. In: Hanski I, Gilpin ME (eds) Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, pp 5–26

Hertzberg K (1997) Migration of Collembola in a patchy environment. Pedobiologia 41:494–505

Hertzberg K, Leinaas HP (1998) Drought as a mortality factor in two pairs of sympatric species of Collembola. Polar Biol 19:302–306

Hertzberg K, Leinaas HP, Ims RA (1994) Patterns of abundance and demography: Collembola in a habitat patch gradient. Ecography 17:349–359

Ims RA (1990) On the adaptive value of reproductive synchrony as a predator-swamping strategy. Am Nat 136:485–498

Ims RA, Stenseth NC (1989) Divided the fruitflies fall. Nature 342:21–22

Ims RA, Yoccoz NG (1997) Studying transfer processes in metapopulations: emigration, migration and colonization. In: Hanski I, Gilpin ME (eds) Metapopulation biology: ecology, genetics and evolution. Academic Press, San Diego, pp 247–265

Kitching RL, Beaver RA (1990) Patchiness and community structure. In: Shorrocks B, Swingland IR (eds) Living in a patchy environment. Oxford University Press, New York, pp 147–165

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260

Leinaas HP (1978) Sampling of soil microarthropods from coniferous forest podzol. Norw J Entomol 25:57–62

Leinaas HP, Fjellberg A (1985) Habitat structure and life history strategies of two partly sympatric and closely related lichen-feeding collembolan species. Oikos 44:448–458

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity. Bull Entomol Soc Am 15:237–240

Levins R (1970) Extinction. In: Gerstenhaber M (ed.) Some mathematical problems in biology. American Mathematical Society, Providence, pp 77–107

Liengen T, Olsen RA (1997) Seasonal and spatial variation in nitrogen fixation in a high arctic area, Ny-Ålesund, Spitsbergen. Can J Microbiol 43:759–769

Lott DF (1984) Intraspecific variation in the social systems of wild vertebrates. Behaviour 88:266–325

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Macfadyen A (1961) Improved funnel-type extractors for soil arthropods. J Anim Ecol 30:171–184

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London

Mengersen KL, Robert CP (1996) Testing for mixtures: a Bayesian entropic approach. In: Bernardo J, Berger J, Dawid A, Smith A (eds) Bayesian statistics 5. Oxford University Press, Oxford, pp 255–276

Nee S, May RM (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. J Anim Ecol 61:37–40

Quinn JF, Hastings A (1987) Extinction in subdivided habitats. Conserv Biol 1:198–208

Rao CR, Toutenburg H (1995) Linear models: least squares and alternatives. Springer, Berlin Heidelberg New York

Robert CP (1996) Mixtures of distributions: inference and estimation. In: Gilks W, Thomas A, Spiegelhalter D (eds). Markov chain Monte Carlo in practice. Chapman and Hall, London, pp 441–464

Rolstad J, Wegge P (1987) Distribution and size of capercaillie leks in relation to old forest fragmentation. Oecologia 72: 389–394

Rosewell JP (1990) Dynamic stability of a single-species population in a divided and ephemeral environment. In: Shorrocks B, Swingland IR (eds) Living in a patchy environment. Oxford University Press, New York, pp 63–74

Shorrocks B (1990) Coexistence in a patchy environment. In: Shorrocks B, Swingland IR (eds) Living in a patchy environment. Oxford University Press, New York, pp 91–110

Simberloff D (1988) The contribution of population and community biology to conservation science. Annu Rev Ecol Syst 19:473–511

Southwood TRE (1977) Habitat, the templet for ecological strategies? J Anim Ecol 46:337–366

Thode HC, Finch SJ, Mendell NR (1988) Simulated percentage points for the null distribution of the likelihood ratio test for a mixture of two normals. Biometrics 44:1195–1201

Titterington DM, Smith AFM, Makov UE (1985) Statistical analysis of finite mixture distributions. Wiley, Chichester

Venables WN, Ripley BD (1994) Modern applied statistics with S-plus. Springer, Berlin Heidelberg New York

Wiens JA (1989) Habitat fragmentation and wildlife populations: the importance of autecology, time, and landscape structure. In: Myrberget S (ed) Transactions of the XIXth International Congress of Game Biology. Norwegian Institute for Nature Research, Trondheim, pp 381–391

Wilcox BA, Murphy DD (1985) Conservation strategy: the effects of fragmentation on extinction. Am Nat 125:879–887

Williams D (1982) Extra-binomial variation in logistic linear models. Appl Stat 31:144–148

Wolff JO, Schauber EM, Edge WD (1997) Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conserv Biol 11:945–956